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Thermal and energetic consequences of nest location and breeding times in Water Pipits (*Anthus spinoletta*)

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Summary

The thermal environment has pronounced effects on the energy costs of thermoregulation and affects an animal's allocation of energy to self-maintenance and parental care. Consequently, the selection of reproductive periods, breeding habitats and nest-sites with a favourable microclimate can be advantageous, especially for birds breeding in harsh environments. In this study on Alpine Water Pipits (*Anthus spinoletta*), we evaluate the importance of spatial and temporal factors on thermoregulatory costs by combining laboratory measurements of metabolic rates under various temperatures with standard operative temperatures (T_{es}) recorded in the field in different microhabitats. Using these measurements we estimate the thermal and energetic consequences of nest locality and timing of reproduction. Our results show: (1) In the morning, T_{es} values were much higher on the east-north-east (ENE) slope of a valley than on the west-south-west (WSW) slope; in the afternoon this pattern was reversed. As a consequence, energy costs (E_{hour}) for thermoregulation on the ENE slope were up to 0.6 RMR (resting metabolic rate at night) lower than on the WSW slope during morning hours and about 0.8 RMR higher during afternoon hours. (2) During the incubation and nestling phases of first and second broods, total energy expenditure for thermoregulation in the daytime ($E_{daytime}$) was 0.2–0.3 RMR higher on the ENE slope than on the WSW slope. (3) Within slopes, $E_{daytime}$ was lower during second broods than during first broods, with differences of 0.06–0.07 RMR during incubation and of 0.32 RMR during nestling care. These differences correspond to the flying costs of females incubating eggs (0.09 RMR) and rearing nestlings (0.25 RMR). We conclude that nest placement in relation to microclimate can improve the female's energy budget, both in terms of the total daily expenditure and its diurnal pattern. From thermal considerations alone, delaying breeding into mid-summer would be advantageous, but this advantage is probably outweighed by the reduced chances for second and replacement clutches and by the necessity to complete moult before migration.

Key words: thermoregulation, energy expenditure, metabolic rate, habitat selection, breeding biology

Zusammenfassung

Thermische und energetische Konsequenzen von Brutplätzen und Brutzeiten bei Wasserpiepern (*Anthus spinoletta*)

Die Umgebungstemperatur beeinflusst den Energieaufwand für die Thermoregulation und bestimmt somit, wie viel Energie ein Tier für die Selbsterhaltung benötigt und wie viel es für Brutpflege aufwenden kann. Daher ist es vorteilhaft, für die Fortpflanzung Zeiten und Orte mit besonders günstigen mikroklimatischen Bedingungen zu wählen. Das gilt insbesondere für Vögel, die in unwirtlichen Biotopen wie z. B. alpinen Regionen brüten. Wir untersuchten den Einfluss von Brutzeit und -ort auf die energetischen Kosten der Thermoregulation am Beispiel einer Population des Wasserpiepers (*Anthus spinoletta*) im Dischmatal bei Davos (Schweiz). Dazu verknüpften wir drei verschiedene Datensätze: a) Ruhestoffwechsel (RMR), gemessen an gefangenen Vögeln unter verschiedenen Temperaturen, b) Umgebungs- und Nesttemperaturen im Freiland während der Brutzeit und c) standardisierte operative Temperaturen (T_{es}), ermittelt mit Kupfervögeln in verschiedenen Mikrohabitaten.

Die Ergebnisse zeigen: (1) In den Morgenstunden sind T_{es}-Werte am Ost-Nord-Ost-Hang (ONO) deutlich höher als am West-Süd-West-Hang (WSW); am Nachmittag sind die Verhältnisse umgekehrt. Als Folge davon sind die Energiekosten (E_{hour}) der Thermoregulation am ONO-Hang in den Morgenstunden bis zu 0.6 RMR niedriger und nachmittags ca. 0.8 RMR höher als am WSW-Hang. (2) In der Bebrütungs- und Nestlingsphase von Erst- und Zweitbruten war der gesamte Energieaufwand für Thermoregulation während der Tagesstunden ($E_{daytime}$) am ONO-Hang 0.2–0.3 RMR höher als am WSW-Hang. (3) Innerhalb jedes Hanges war $E_{daytime}$ bei Zweitbruten niedriger als bei Erstbruten: 0.06–0.07 RMR während der Bebrütung der Eier und 0.32 RMR während der Nestlingsphase. Diese Größenordnungen entsprechen den Flugkosten von Weibchen während der Bebrütungszeit (0.09 RMR) bzw. der Jungenaufzucht (0.25 RMR).

Unsere Ergebnisse belegen, dass die Wahl von klimatisch günstigen Habitaten die Energiebilanz von Brutvögeln verbessern kann, sowohl in Hinblick auf den täglichen Gesamtaufwand als auch bezüglich der Verteilung des Energieverbrauchs über den Tag. Aus thermoregulatorischen Gründen wäre auch eine zeitliche Verlagerung des Brutgeschäfts in die Sommermonate (Juli, August) vorteilhaft. Das würde jedoch die Möglichkeiten für Ersatz- und Zweitbruten verringern und die Zeit für die Mauser vor dem Herbstzug verkürzen. Da in unserem Untersuchungsgebiet diese Faktoren für eine erfolgreiche Fortpflanzung eine größere Bedeutung haben als der Energieaufwand für die Thermoregulation, ist der frühe – energetisch 6–32 % teurere – Brutbeginn der Vögel sinnvoll.

Introduction

Breeding birds not only have to allocate energy to self-maintenance but also to parental care. Inadequate care can reduce reproductive success (e. g. Wright & Cuthill 1989, Dijkstra et al. 1990, Martins & Wright 1993, Pettifor 1993); failure to allocate enough energy to self-maintenance can impair survival (e. g. Nur 1984, Partridge 1989, Dijkstra et al. 1990). With an upper limit to sustained daily energy expenditure (DEE) of 4–7 times basal metabolic rate (BMR) (Drent & Daan 1980, Bryant & Tatner 1990), optimal allocation of energy between the two demands will be important, especially in conditions of low food availability (affecting energy intake) and/or unfavourable climatic conditions (affecting energy expenditure).

High temperatures and intense solar radiation, combined with high levels of humidity in tropical habitats and low water availability in arid environments, may force birds to abandon foraging activity for many hours a day (Walsberg 1993, Wolf et al. 1996). This will reduce the energy intake of parents and their offspring (Austin 1976, Clark 1987). Low temperatures, especially when coupled with strong winds and low solar radiation, will lead to convective and radiative heat loss and, thus, increase the level of maintenance metabolism (Webster & Weathers 1988, Wolf & Walsberg 1996). Since thermoregulation can account for as much as 20–40 % of the DEE (Ettinger & King 1980, Biedenweg 1983, Finch 1984, Masmann 1986, Webster & Weathers 1990, Weathers & Sullivan 1989, Piersma & Morrison 1994), minimising thermoregulatory requirements during breeding would allow parents to allocate more energy to brood care.

Some species have evolved specific physiological responses for coping with extreme climatic conditions. BMR, for instance, tends to correlate with latitude, leading to reduced food requirements and less evaporation in the tropics and to increased rates of endogenous heat production in temperate and arctic zones (Marschall & Prinzinger 1991, Schleucher et al. 1991, Weathers 1979, 1997, Weathers & Greene 1998). Usually, however, selection seems to have produced behavioural responses for reducing the negative effects of adverse climates; microhabitat selection is a typical example of this (Calder 1973, Walsberg & King 1978, Walsberg 1981, 1993, Webb & King 1983, With & Webb 1993, Zerba & Morton 1983). Some species even create more favourable thermal conditions themselves, e. g. by social roosting (Walsberg 1990, Du Plessis et al. 1994, Du Plessis & Williams 1994).

Among the most extreme breeding habitats are areas of high latitudes and altitudes. On arctic tundras and on mountains above the treeline, average air temperatures are low and wind speeds often high. Short-term fluctuations can be extreme, ranging from intense solar radiation and very high temperatures on clear days to spells of frost and snowfall even in summer (Franz 1979). These conditions usually elevate the DEE of breeding birds over those of comparable species reproducing under less extreme conditions (Ettinger & King 1980, Piersma & Morrison 1994; for rare exceptions see Tatner & Bryant 1993). Thus, microhabitat selection – through its effect on thermoregulatory costs – can be assumed to be an important determinant of reproductive success. This is particularly true for small birds, which have high mass-specific rates of energy expenditure, owing to their large surface-area-to-volume ratio.

In the current study we examine the thermal and energetic effects of microclimate for ground nesting Alpine Water Pipits (*Anthus spinoletta*). By combining measurements of air temperature, solar radiation and wind speed from the field with those of heat loss under standard conditions in the lab, we estimate the thermal and energetic effects for birds breeding during different times of the season and at localities differing in vegetation and solar radiation. Such comparisons are particularly important for arctic and alpine species with their spatially and temporally limited breeding options; but the importance of energetic expenditure relative to such limitations is poorly known.

Methods

Study area and birds

The study was conducted during the breeding season 1992 in the Dischmatal near Davos, Kanton Graubünden, Switzerland. The study area, a cross section through the valley, covers about 200 ha and lies above the treeline (elevation 1 820–2 400 m). Dwarf shrubs are the predominant vegetation structures on the slopes. On the ENE oriented slope of the valley rhododendron bushes (*Rhododendron ferrugineum*) dominate the vegetation. On the WSW oriented slope juniper (*Juniperus communis*) and heather (*Calluna vulgaris*) are the most abundant shrub species. Meadows, which are used to graze cattle or to make hay, characterise the valley floor.

The climate is relatively continental with monthly mean temperatures of –5.6 °C in January and 11.9 °C

in July and mean annual precipitation of 878 mm (10year means of 1980–1989, measured at Davos-Dorf by Schweizerische Meteorologische Anstalt, SMA).

Solar radiation differs considerably between the two slopes of the valley: Moser et al. (1986) estimated solar radiation by a model, which included information about topography, position of the sun and meteorological data. From this model, they produced a radiation map of the valley for the time period between the 16th of May and 15th of July. They distinguished four categories of radiation: 0–177 kW/(ha*y), 178–197 kW/(ha*y), 198–211 kW/(ha*y) and 212–240 kW/(ha*y). According to the radiation map, the ENE slope of the valley receives less than 197 kW/(ha*y) whereas the WSW slope receives between 178 and 211 kW/(ha*y).

Water Pipits, small insectivorous passerines, are common breeders in the Alps above the treeline (Glutz von Blotzheim & Bauer 1985). At our study site, they return from their wintering areas in April. Nesting starts in late May or early June. Only the females build the nests, which are made of grass. The nests are built on the ground and are more or less overhung by rock, sod, or vegetation. Clutch size ranges from 3 to 6 eggs, with clutches of 4 and 5 being the most common. The females incubate the eggs and the males provision the attending females with food. On average, incubation takes 15 days. The nestlings are fed by both parents but only the females brood the young. On about the 15th nestling day the chicks fledge. Under favourable weather conditions second broods are initiated. In 1992 the incubation of most first broods was started on 2 June. Median hatching day was 17 June and median fledging day 30 June. The incubation of second broods was initiated on 5 July, hatching took place at 19 July and median fledging day was 2 August. Further information on the study area and the biology of the birds is given by Frey-Roos et al. (1995), Bollmann et al. (1997), Brodmann et al. (1997a,b), Rauter & Reyer (1997), Reyer et al. (1997), Rehsteiner et al. (1998) Brodmann & Reyer (1999) and Rauter et al. (2000).

Microclimate measurements

General weather conditions were recorded in terms of wind speed (U) and air temperature (T_a), measured according to international standards every 10 minutes at the weather station of Davos-Dorf by the Schweizerische Meteorologische Anstalt (SMA). These 10 minute recordings were used to calculate hourly means. In the study area, microclimatic differences between vegetation and nests and between the two slopes of the valley were determined from 08.00–19.00 on clear days between 15 July and 29 August 1992. Our technical equipment allowed us to measure U, T_a and T_e (see below) simultaneously in two vegetation types and at two nests per day, both randomly selected. In total, we have one-day measurements in the vegetation from 12 sites on the ENE slope and 15 sites on the WSW slope. These sites were evenly distributed on both slopes. In the vegetation, U was recorded with a cup anemometer (measuring range 0.2–75 m/s, Type AN1, Delta-T Devices Ltd., Cambridge, U. K.) and T_a with a NiCr-Cr thermocouple (Thiele, Ingenieur Büro für Messtechnik GmbH, München, FRG). Both measurements were taken between shrubs, 20cm above ground. For nests, U could not be measured directly; but in ground nests, comparable to those of Water Pipits, U_{max} ranges from 0.1–0.25 m/s (With & Webb 1993). Hence, we assumed an intermediate value of 0.15 m/s for our calculations. T_a at nests was measured directly – in 11 nests on the ENE slope and in 6 nests on the WSW slope – by a thermocouple (NiCr-Cr, Thiele) placed underneath the nest cover, above the centre of the nest cup. Measurements of T_a, U and T_{es} (see below) were stored by Rustrak data loggers (Thiele). One-minute recordings were used to calculate hourly means.

Operative and standard operative temperatures

Complex thermal environments can be described by single indices, the operative temperature (T_e) and the standard operative temperature (T_{es}). T_e represents the equilibrium temperature a metabolically inert organism would attain in a given combination of air temperature, wind speed and solar radiation (Bakken et al. 1985, Bakken 1992). We measured T_e with unheated taxidermic mounts,

constructed following the techniques described in Bakken & Gates (1975) with some modifications. Four Water Pipits were skinned. The skinned bodies were set in an upright position and a plaster mould was made from each body. From these moulds paraffin casts were produced. A thin copper layer was deposited on the paraffin cast by F. Wilhelm (Galvano-Studio, Zug, CH). Afterwards the paraffin was melted out and the skin was stretched over the copper cast. As the mounds had no legs, each mount was attached to a wooden peg, which was used to fix the mount in the ground in an upright position. Internal temperature (T_e) was measured using a NiCr-Cr thermocouple (Thiele) placed in the centre of the abdominal region of the hollow cast. To measure T_e in the vegetation, the mounts were placed on the ground between shrubs, where Water Pipits usually forage. In the nests, the mounts were positioned in such a way that they resembled incubating or brooding Water Pipits. As incubating and brooding Water Pipits were always orientated down hill, the mounts were faced in the same direction, both in the nest and in the vegetation. Since different taxidermic mounts, placed under identical thermal conditions, can markedly deviate in their recordings of operative temperature (Walsberg & Wolf 1996), the four pipit casts were evenly distributed in space and time.

T_{es} is defined in the same way as T_e, but for a reference environment with fixed convection (i. e. wind speed) conditions. T_{es} represents air temperature within a standard metabolic chamber that produces a degree of thermal stress equivalent to that produced by a natural environment. Such standardisation is required when the effects of different microclimates (e. g. on different slopes) are to be compared. T_{es} was calculated using the equation given in Bakken (1990): $T_{es} = T_b - (1 + 0.26\sqrt{U})\,(T_b - T_e)$; where T_b = body temperature (see below).

Energy expenditure in relation to temperature

Energy expenditure of 8 captive Water Pipits (4 males and 4 females) was determined between 28 July and 1 September 1993, i. e. towards the end of the period when some free-living Water Pipits raise their second broods. Several studies have shown that energy expenditure is a function of body mass and body composition which, in turn, change during the season with hormone levels, moult, fat storage and other preparations for migration (e. g. Piersma et al. 1996, Scott et al. 1996). Yet, for various reasons we believe that the energy values mainly obtained in August provide a valid basis for calculating the thermoregulatory costs of birds breeding earlier during the season: (a) None of the 8 Water Pipits was moulting during the experiment. (b) Migration does not take place before October and involves only short distances; hence substantial physiological preparations for migration were unlikely. (c) The average morning body mass of the experimental birds was very close to that of 153 breeding birds captured in the field between 17 May and 2 August (22.8 ± 2.0 g versus 22.5 ± 1.8).

Energy expenditure was measured under the following temperatures (day/night): 1.0/0.5, 9.0/8.0, 17.0/16.0, 24.5/24.0, 26.5/26.0, 28.0/27.5, 30.0/29.5 and 31.5/31.0 °C. Following the technique of Prinzinger (1988), oxygen consumption was measured in an open flow system with a paramagnetic oxygen analyser (MAGNOS 4G, Hartmann & Braun, Zürich, CH). During the measurements, effluent air was adjusted at 30 l/h (air-dried) with a flow meter (Type 1100, Wisag AG, Zürich, CH). All gas volumes were reduced to STPD conditions. Energy equivalent per volume oxygen was taken as 20.1 J/ml O_2 (Blaxter 1989). All measurements were done in a temperature chamber ($1.00 \times 0.55 \times 0.66$ m, Type 2233, Köttermann GmbH & Co, Uetze-Häningen, FRG) regulated to ± 1 °C. During the experiments, the birds were kept in a plexiglas box ($25 \times 15 \times 17$ cm) provided with food and water. Each bird was exposed to each temperature for 24 hours under a light-dark cycle (light phase: 5.00–19.00 CET). At 6.30 the birds were fed, body temperature (T_b) and body weight were measured

and the temperature in the chamber was changed. Then, the system was allowed to calibrate for about 1 3/4 hours before oxygen consumption was measured from 8.30 until 16.30. Then the birds were fed again and body mass was taken a second time, before oxygen consumption at night was measured between 20.00 and 5.00 under about the same temperature conditions as in the daytime. When not used for the experiments, all birds were kept together in an outdoor aviary with access to an indoor aviary. They were fed with dried insects and a mixture of cream cheese and ox heart.

Calculations and statistics

Since the number of recording devices for U, T_a and T_e was limited, we could not simultaneously measure these variables for all vegetation types and nests, nor for the two slopes and for both the incubation and nestling phases. Consequently, any calculation of temporal and spatial differences in T_{es} would have been confounded by different weather conditions on different days. To solve this problem we calculated T_{es} via relative values of U, T_a and T_e. Relative U and relative T_a are the differences between U and T_a, respectively, measured in the vegetation or the nests and the corresponding values simultaneously measured at the weather station. Relative T_e is the difference between the T_e in the vegetation or in the nests and the simultaneously measured T_a at the weather station. T_{es} was then calculated in the following way: (1) T_a and U, measured at the weather station, were determined hourly for all breeding phases. (2) Relative T_e of vegetation and nests of either slope were added to the hourly T_a, which yielded the absolute T_e. (3) For vegetation, relative U-values were added to the hourly U at the weather station, for nests U was assumed to be 0.15 m/s (see above).

From the hourly T_{es} values, representing air temperature under (standardised) thermal conditions in the field, and the hourly energy expenditure measured in the laboratory under different T_a, we first calculated the hourly energy expenditure (E_{hour}) of a bird staying exclusively in the vegetation or in the nests. The results were then weighted by the proportion of time a female Water Pipit actually spends in the vegetation and the nest. These values are 25 % and 75 %, respectively, during incubation and 85 % and 15 %, respectively, during nestling care (Rauter 1996).

At first sight, energy calculations combining metabolic rates under different T_a in the daytime with T_{es} may appear problematic, because estimates of T_{es} with Bakken's (1990) equation assume that birds are resting in the dark. However, BMR and RMR are known to be higher during daytime than during nighttime (Aschoff & Pohl 1970). This pattern is also obvious from our data, which produce almost identical slopes in the energy-temperature relationship during day and night (see Fig. 2). Therefore, and because birds in the field move around and forage, we considered the daytime metabolic rates of slightly active lab birds to be a more realistic reference. Moreover, all our results and conclusions are based on comparisons between values calculated in the same way. Hence, observed differences between the two slopes and between early and late seasons, respectively, are unlikely to be systematically affected by our mode of calculation.

Temporal differences between breeding phases and spatial differences between slopes or nests and vegetation were statistically tested with t-tests and one-way analyses of variance (ANOVA). Where separate comparisons are made for each hour, significance levels were Bonferroni corrected. All statistical analyses were performed using the programme SAS (SAS Institute Inc. 1985).

Results

Wind speed and air temperature

Wind speed showed a strong daytime pattern, both at the weather station and in the vegetation. Starting with low values in the morning (station: < 1.0 m/s, vegetation: < 0.5 m/s) average velocity increased to maximum values between 13.00 and 17.00 (station: 5 m/s, vege-

tation: 1 m/s) and then dropped again. Overall, average daily wind speeds measured in the vegetation and at the weather station differed neither between the ENE and the WSW slope ($t = 0.92$, $df = 20$, $p = 0.370$) nor between the four breeding phases (ANOVA: $F = 1.89$, $df = 3,51$, $p = 0.142$). On an hourly basis, wind velocity did not differ either with site (t-tests: $p > 0.05$ for all hours), or with season (ANOVAs: $p > 0.05$ for all hours). During the incubation of first and second broods and during the nestling care of first broods, hourly averages of air temperature rose from 8 °C at 08.00 to a maximum of 14 °C between 13.00 and 16.00, with no significant differences among the three phases. During nestling care of second broods, however, the corresponding values (13–21 °C) were significantly higher (separate one-way ANOVAs including all four breeding periods for each hour, all $p < 0.001$, Scheffe test for differences among breeding periods). In the morning (08.00–10.00) hourly averages were 3.5–7.4 °C higher on the ENE slope than on the WSW slope, in the afternoon (12.00–18.00) this pattern was reversed, with the WSW slope being 5.3–11.1 °C warmer (t-tests: $p < 0.05$ for all hours). On the ENE slope temperatures in vegetation and nests were equal except in the late afternoon (16.00 : 18.00), when the nests were 2.8–4.7 °C warmer than the vegetation. On the WSW slope, temperature was 2.2–6.5 °C higher in the vegetation than in the nests in late morning and early afternoon (08.00–13.00; t-tests: $p < 0.05$ for all hours); but later on there was no difference between vegetation and nests (t-tests: $p > 0.05$ for all hours).

Standard operative temperature

The climatic conditions described above translate into the standard operative temperatures (T_{es}) in vegetation and nests shown in Fig. 1a–d. In all four breeding phases both T_{es} showed the same pattern: they reached their maxima on the ENE slope in the morning and on the WSW slope in the early and late afternoon, respectively. Maxima were always much lower on the ENE slope than those on the WSW slope. At both slopes, T_{es} in the vegetation was higher than T_{es} in the nests during the late morning, whereas in the afternoon the pattern was reversed. During the nestling phase of second broods, T_{es} in vegetation and T_{es} in nests were – at any hour – about 5 °C higher than the corresponding values during the earlier breeding phases.

Energy expenditure in the laboratory

The respiratory measurements in the laboratory revealed a minimum energy expenditure of 2.052 kJ/h, which was achieved at night at temperatures above 25 °C (Fig. 2). This represents the resting metabolic rate (RMR), defined as the heat production of a bird at rest, under thermoneutral conditions, but not in a postabsorptive state which is required in the case of basal metabolic rate (BMR; e. g. Whittow 1986). However, with feeding around 17.00 and energy measurements taken between 20.00 and 05.00 (see Methods), nightly RMR-values probably are very close to BMR. Below 25 °C, energy expenditure E (kJ/h) during the night increased with decreasing temperature T_a (°C) according to the equation: $E = 4.109 - 0.080 * T_a$. In the daytime, the relation between E and T_a was $E = 5.953 - 0.087 * T_a$, with no obvious thermoneutral zone within the tested temperature range.

The mean body temperature (T_b) of the eight tested birds was 42.5 ± 0.4 °C (range 41.9–43.1 °C). Their body weight was 22.8 ± 2.0g (range 19.7–25.3) in the morning and 24.0 ± 2.0 g (range 20.8–26.4) in the evening. At the three temperatures below the thermoneutral zone (0 °C, 8 °C and 16 °C), Water Pipits lost on average 1.4 ± 0.5 g, 1.1 ± 0.3 g and 1.0 ± 0.3 g, respectively, overnight. This was 6 %, 5 % and 4 %, respectively, of the mean morning body weight.

Energy expenditure in the field

From the energy measurements in the laboratory and the operative temperatures recorded in

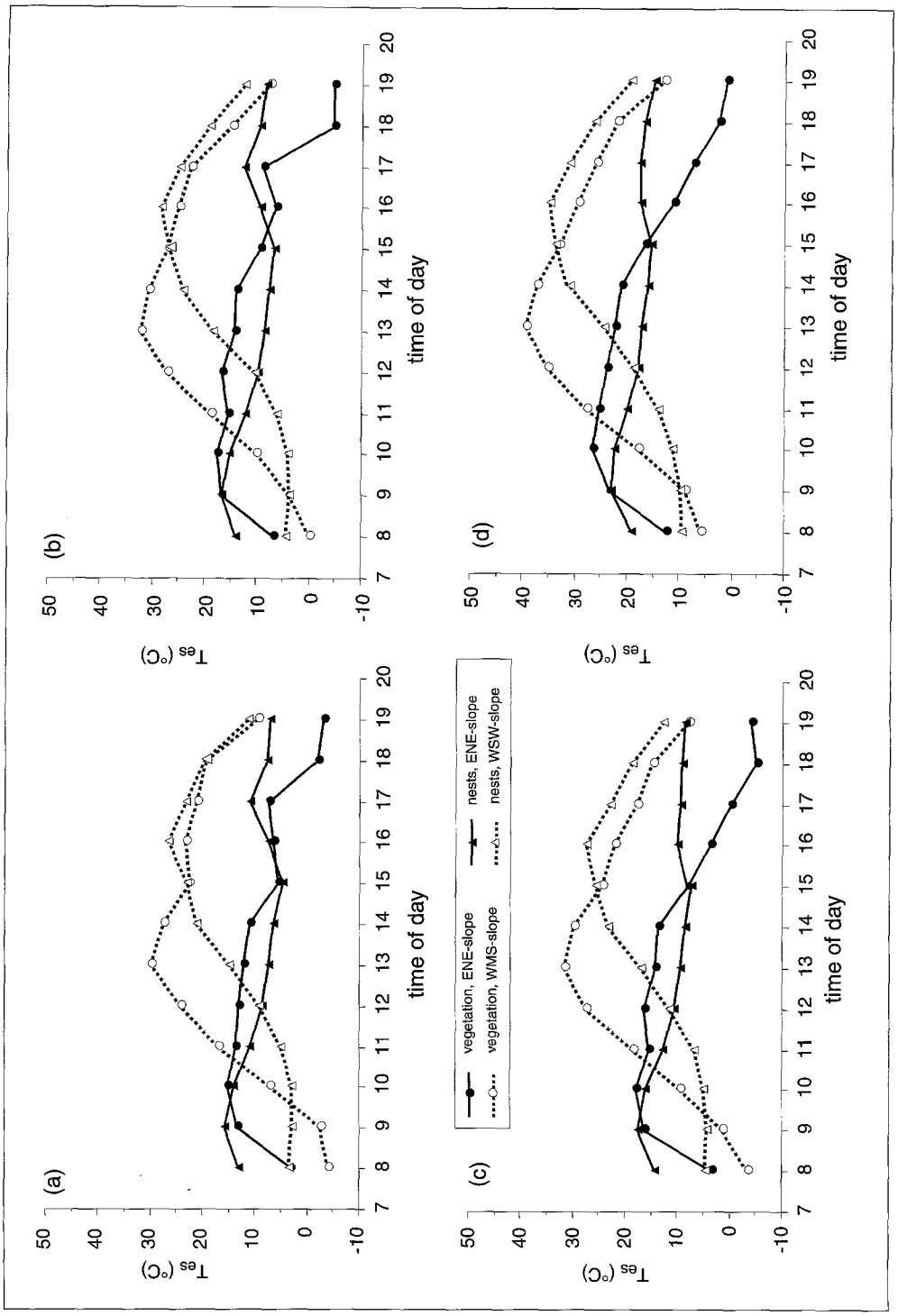
(a)
(b)
(c)
(d)
T_{es} (°C)
time of day
vegetation, ENE-slope
vegetation, WMS-slope
nests, ENE-slope
nests, WSW-slope

Fig. 1 Standard operative temperature (T_{es}) in the vegetation and in the nests on the ENE and the WSW slope in relation to time of the day. a) Incubation phase of first broods, b) incubation phase of second broods, c) nestling phase of first broods and d) nestling phase of second broods. Calculation of T_{es} is based on Bakken's (1990) equation given under methods and the mean body temperature (T_b) of 42.5 °C recorded during the laboratory energy measurements.

Abb. 1. Standard operative Temperatur (T_{es}) in der Vegetation und in Nestern am Ost-Nord-Ost Hang (ENE slope) und West-Süd-West Hang (WSW slope) in Beziehung zur Tageszeit (time of day). a) Bebrütungsphase bei Erstbruten, b) Bebrütungsphase bei Zweitbruten, c) Nestlingphase bei Erstbruten und d) Nestlingphase bei Zweitbruten. T_{es} wurde nach der im Methodenteil aufgeführten Formel von Bakken (1990) errechnet. Die dafür erforderliche mittlere Körpertemperatur der Vögel (T_b) stammt aus den Energiemessungen im Labor und betrug 42.5 °C.

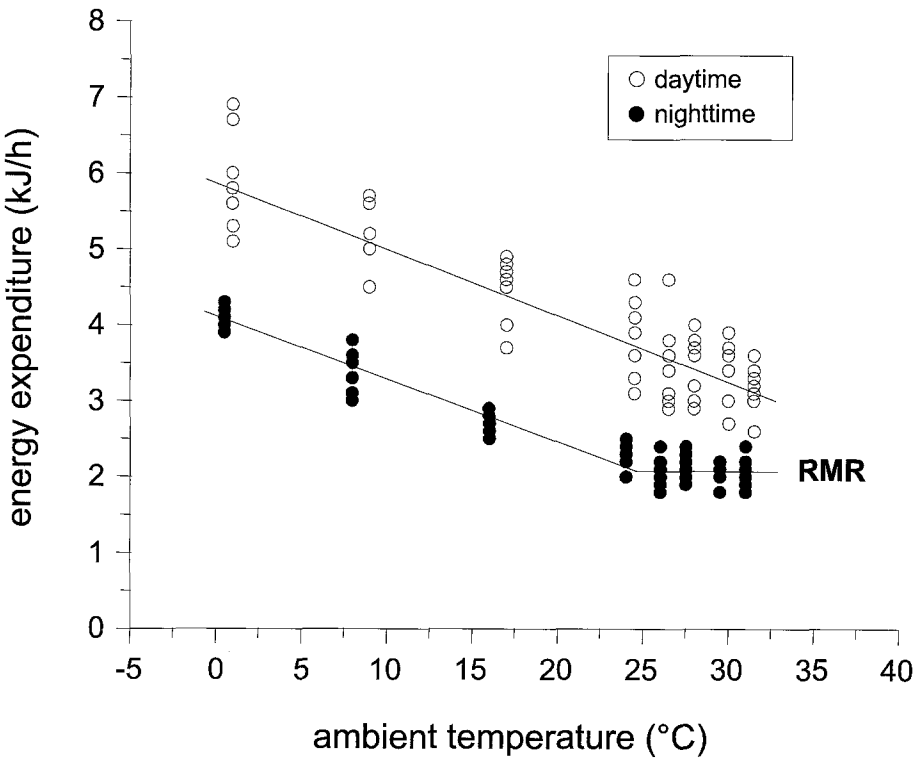

Fig. 2 Energy expenditure E (kJ/h) in relation to ambient temperature (T_a) in the daytime and at night-time. During the day, the relation between E and T_a is $E = 5.953–0{,}087*T_a$; at night the corresponding relation is $E = 4.109–0.080*T_a$ for temperatures below 25 °C. Above 25 °C, resting metabolic rate (RMR) equals 2.052 kJ/h (horizontal line) which is used as a reference in Figures 3 and 4.

Abb. 2. Energieverbrauch (E kJ/h) in Beziehung zur Umgebungstemperatur T_a (°C) am Tag und in der Nacht. Die Beziehung zwischen E und T_a während des Tages wird beschrieben durch die Gleichung $E = 5.953–0{,}087*T_a$. Nachts lautet die entsprechende Gleichung $E = 4.109–0.080*T_a$ für Temperaturen unter 25 °C; darüber beträgt der Ruhestoffwechsel (RMR) 2.052 kJ/h (horizontale Linie). Dieser Wert liefert die Vergleichsbasis für die Daten in Abb. 3 und 4.

the field we estimated – separately for each breeding phase and either slope – the hourly energy expenditure (E_{hour}) of birds. The calculations reveal that on the ENE slope E_{hour} was lowest in mid morning and thereafter increased steadily until the evening (Fig. 3). Conversely, on the WSW slope, E_{hour} decreased from highest values in the morning to minimum expenditure in the early afternoon and then rose again towards the evening. Differences between the slopes were largest in mid morning, when E_{hour} on the WSW slope was as much as 0.6 RMR higher than on the ENE slope, and in the late afternoon when on the ENE slope E_{hour} was about 0.8 RMR larger than on the WSW slope (Fig. 4a).

Total energy expenditure for thermoregulation and basal metabolism in the daytime ($E_{daytime}$) was estimated by summing up the 12 individual E_{hour} averages. The resulting values ranged from 46.1–61.9 kJ (Fig. 3), with differences related to time and space (Fig. 4b). In terms of space, $E_{daytime}$ was 10–16 % (or 0.21–0.33 RMR) higher on the ENE slope than on the WSW slope during all four breeding phases. In terms of time, daily energy expenditure was 2 % (incubation) to 16 % (nestling care) higher for females with first than for those with second broods; this corresponds to a difference of 0.06–0.32 RMR.

Discussion

T_{es} and E_{hour} showed the same general pattern at daytime in all breeding phases, but differed considerably between slopes. In the morning T_{es} was higher and E_{hour} was lower on the ENE slope than on the WSW slope (Figs. 1, 3). In the afternoon this relationship was reversed. A reduced E_{hour} in the morning may be advantageous, because the nightly loss of body mass can be compensated more rapidly. Temperature measurements in nests of first broods in 1991 and 1992 revealed that average nighttime temperatures ranged from 4.5 to 13.3 °C and they did not differ between the slopes (Rauter 1996). Water Pipits kept overnight in the temperature chamber at similar temperatures lost between 1.0 g (at 16 °C) and 1.4 g (at 0 °C), which corresponds to 4–6 % of their average body weight in the morning (22.8 ± 2.0 g). Although this weight loss overnight is at the lower end of the diurnal body weight fluctuations which ranges from 5 to 12 % (Clark 1979, Lehikoinen 1987, Haftorn 1989, Rogers & Rogers 1990), for incubating females even this moderate loss may be critical for their energy budget in the morning. Incubating females have not only to allocate time and energy to self-maintenance, but also to parental care. Foraging and attending eggs are conflicting demands, hence energetic constraints can result in prolonged foraging bouts and thus reduce attentiveness (e. g. Lyon & Montgomerie 1985, Moreno 1989, Smith et al. 1989). This can lead to suboptimal thermal conditions for the eggs (e. g. Johnson & Cowan 1974, Zann & Rossetto 1991, Williams 1993) and cause immediate death of the embryo, sublethal teratogenic effects or retard development (Webb 1987). There is some evidence in the Water Pipit that low temperatures strain the incubating females' time and energy budgets (Rauter 1996, Rauter & Reyer 1997): (1) The length of the inattentive period increased with decreasing temperature and (2) the length of the incubation period increased as the average mean daily air temperature decreased.

Once the eggs have hatched parents have to balance their time and energy expenditure between self-maintenance, brooding and feeding chicks. In Water Pipits there is no evidence that temperature constrains parental care for older nestlings: male feeding patterns are not related to temperature and females even show a tendency to increase their feeding rates with decreasing temperature (Rauter et al. 2000), indicating that the higher thermostatic demands in the morning on the WSW slope do not affect their ability to regain the body weight lost overnight. But the daytime pattern of nest temperature has a significant effect on nestling survival: successful nests on the ENE slope fledged significantly more young than

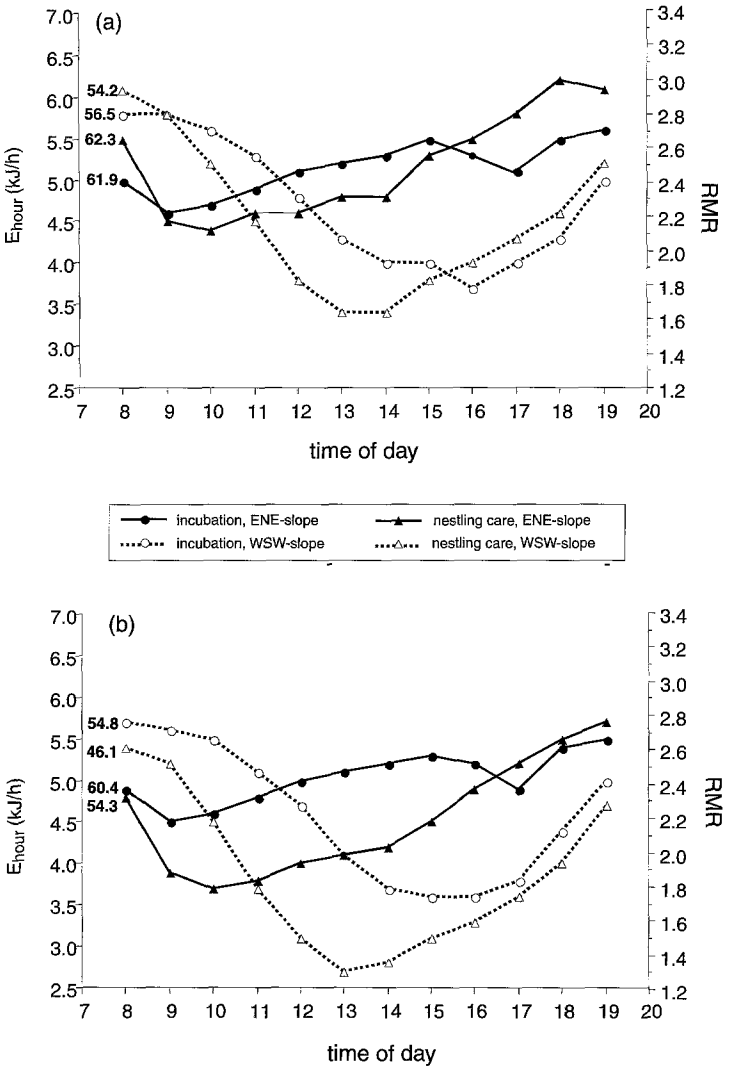

Fig. 3. Energy expenditure (kJ/h) for resting metabolism and thermostatic demands during incubation and nestling care on the ENE and WSW slopes in relation to time of the day. a) first broods, b) second broods. On the left y-axes, E_{hour} is given in kJ/h, on the right axes as multiples of resting metabolic rate (RMR) at nighttime. The four bold numbers in each of the two graphs give the daytime energy expenditure ($E_{daytime}$) which is the sum of the 12 E_{hour} values from the adjacent curves.

Abb. 3. Energieverbrauch (kJ/h) für Ruhestoffwechsel und Aufrechterhaltung der Körpertemperatur in Beziehung zur Tageszeit (time of day). Abb. a) zeigt die Werte für Erstbruten, Abb. b) die für Zweitbruten. In beiden Abbildungen sind die Werte für die Bebrütungsphase (incubation) und die Nestlingsphase (nestling care) sowie für den Ost-Nord-Ost Hang (ENE slope) und den West-Süd-West Hang (WSW slope) getrennt aufgetragen. Die linken y-Achsen zeigen E_{hour} in kJ/h, die rechten E_{hour} als Vielfaches des Ruhestoffwechsels (RMR). Die fettgedruckten Zahlen geben den Tagesenergieverbrauch an ($E_{daytime}$). Er ist die Summe aus den 12 E_{hour}-Werten der entsprechenden Kurven.

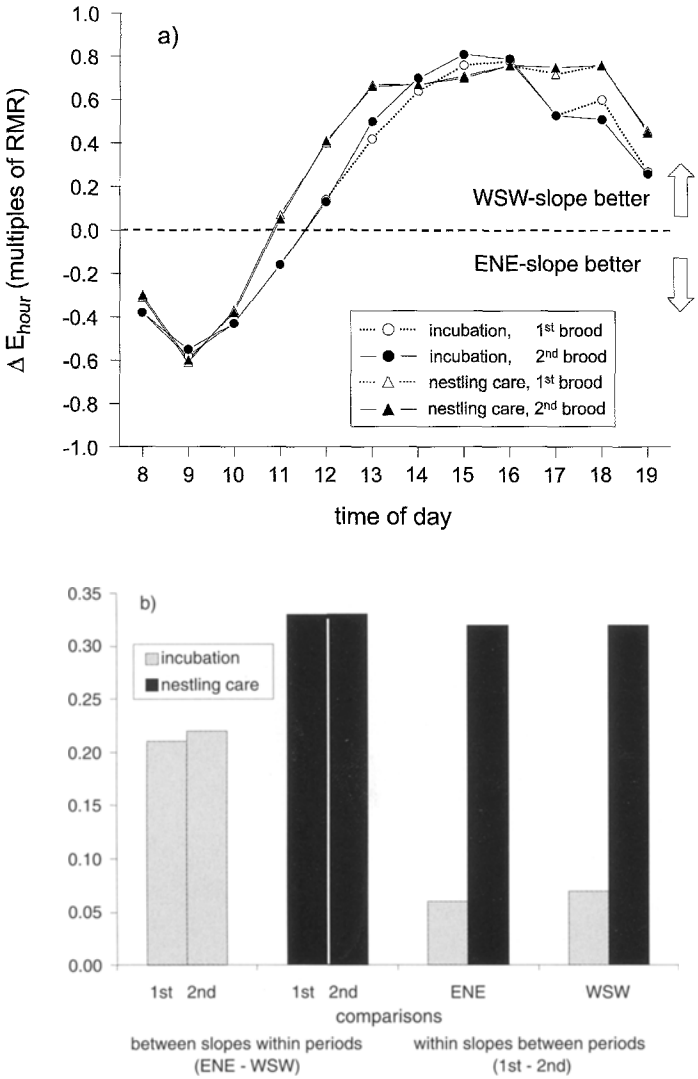

Fig. 4. Comparisons between energy expenditure for thermostatic demands of birds breeding at different locations and times. a) Differences in hourly expenditures (ΔE_{hour}) between the ENE and the WSW slope. The broken horizontal line indicates no difference between the two slopes. b) Differences in daily expenditures ($\Delta E_{daytime}$) within corresponding breeding periods between slopes and between periods within slopes. All differences are calculated as $E_{ENE} - E_{WSW}$ and expressed in multiples of resting metabolic rate (RMR).

Abb. 4. Vergleich des Energieaufwandes für die Aufrechterhaltung der Körpertemperatur bei Vögeln, die zu verschiedenen Zeiten und an verschiedenen Orten brüten. a) Unterschiede im Energieaufwand pro Stunde (ΔE_{hour}) zwischen Ost-Nord-Ost- und West-Süd-West-Hang in Beziehung zur Tageszeit. Die gestrichelte horizontale Linie markiert keinen Unterschied. b) Unterschiede im Energieaufwand während des Tages ($\Delta E_{daytime}$) zwischen Hängen innerhalb vergleichbarer Brutphasen und zwischen Brutphasen innerhalb der Hänge. Alle Unterschiede wurden als $E_{ENE} - E_{WSW}$ berechnet und sind als Vielfaches des nächtlichen Ruhestoffwechsels (RMR) dargestellt.

those at WSW slope (Rauter 1996) although food availability is significantly lower on the ENE slope ($p = 0.004$, $df = 112$, $t = 2.934$; P. Brodmann, unpubl. data). The most likely explanation for this difference in survival seems to be a combined effect of exposure of the broods on the WSW slope to colder temperatures in the morning and heat stress in the afternoon. Thus, from thermal considerations, the ENE slope seems to be the more favourable one during both incubation and nestling care. During incubation the higher morning temperatures reduce the females' thermostatic demands and slow down the cooling rate of eggs thus allowing longer foraging bouts and a more rapid compensation of nightly body mass loss. During the nestling care higher temperatures in the morning reduce the nestlings' thermostatic costs and cooling rate and the lower afternoon temperatures reduce the heat stress on the chicks.

The total energy expenditure for thermoregulation and maintenance metabolism in the daytime ($E_{daytime}$) was higher on the ENE slope than on the WSW slope in all breeding phases and within each slope higher for first then for second broods. (Fig. 4). The spatial differences in $E_{daytime}$ ranged from 0.2–0.3 RMR; the seasonal differences amounted to 0.06–0.07 RMR during incubation and to 0.32 RMR during nestling care. The lower values almost equal the mean flight costs of females during the incubation period (mean = 0.09 RMR, range 0.02–0.3, $n = 18$); the higher values are of the same order as the mean flight costs of females rearing nestlings (mean = 0.25 RMR, range 0.06–0.46, $n = 18$; both estimated from the time spent to fly back and forth between nest and foraging sites, multiplied by 11.7 RMR; Carlson & Moreno 1992).

Thus, reproductive success seems to be less affected by the total $E_{daytime}$ – which is higher on the ENE than on the WSW slope – than by energy expenditure at certain times of the day. Relatively low E_{hour} values on the ENE slope during the morning may markedly lessen the females' conflict in allocating energy to self maintenance and parental care at times when low food availability forces female Water Pipits to work harder for foraging (Rauter 1996, Rauter & Reyer 1997). Combined with the more favourable microclimate for nestlings (see above), this results in the prediction that birds should prefer the ENE slope for breeding. The prediction is supported by the fact that during all four years of a field study territory density was 50–100 % higher on the ENE- than on the WSW slope (Bollmann 1996, A. R. Schläpfer unpubl. data). Similarly, a delay of breeding until the second half of the reproductive season would also reduce thermostatic demands and, hence, improve energy allocation to nestlings. However, such a delay was not observed: 96 % of first broods were produced in the first half of the season (Bollmann et al., in prep.). We see several, not mutually exclusive, reasons for this discrepancy.

(1) Annual variation in climate: In 1992 the weather conditions during the period of second broods (July), were exceptionally good, whereas conditions, especially air temperature, during the period of first broods (June) were similar to the long-term averages (Bollmann, 1996). Therefore, a delay of breeding until the second half of the season will, on average, reduce the energy costs for thermoregulation to a lesser extent than indicated by the present study. Yet, delaying would still be advantageous in terms of thermostatic costs.

(2) Nest loss: The most important factors determining reproductive success in Water Pipits are predation and total nest loss through late snow fall (Bollmann et al., in prep.; Rauter et al., in prep.). A delay of breeding would reduce the probability to successfully rear a second clutch or, in the case of nest failure, a replacement clutch. Since predation, especially by adders (*Vipera berus*), is much higher on the WSW than on the ENE slope, the higher territory density at the latter may also reflect predator avoidance.

(3) Moult and migration: Late breeding in Water Pipits is probably constrained by the need to moult before migration.

(4) Methodological artefacts: The above statements about energetically more or less favourable habitats and seasons, respectively, ignore one potentially important energy source for thermoregulation: heat generated as a by-product of physical activity and feeding (Masmann et al. 1988, Webster & Weathers 1990, Zerba & Walsberg 1992). The significance of such compensatory mechanisms for the energy budget cannot be calculated from (inactive) taxidermic mounts. This is one reason why in recent years scientists have increasingly used direct energy expenditure measurements through the doubly-labelled water technique (DLW; Lifson & McLintock 1966) However, not all birds tolerate the extensive handling associated with this technique. For instance, Weathers et al. (1996) found that out of 90 individuals from 16 species, which were injected with DLW, kept for a while and then blood sampled, only 19 individuals from 5 species could be recaptured for the necessary second blood sampling. In our study, all five birds originally subjected to the DLW technique left the breeding area and were never seen again.

In such sensitive species, indirect measures of field metabolic rates are still the only possibility. Moreover, activity not only generates heat, it also disrupts the aerodynamic boundary and plumage insulation layers and, hence, increases convective heat loss (Zerba & Walsberg 1992). These two opposing effects probably explain why heat as a by-product of activity does not fully compensate for thermoregulatory costs, especially not in the range of temperatures experienced by arctic and alpine birds (Webster & Weathers 1990). Since simultaneous application of direct and indirect measures of energy expenditure have confirmed the importance of standard operative temperatures to daily energy expenditure (Piersma & Morrison 1994), the use of taxidermic mounts is encouraged, especially in cold climates.

In conclusion, although our energy measurements may not yield the precise absolute energetic costs for thermoregulation in Water Pipits, they clearly reveal the relative spatial and temporal differences, which are related to thermal conditions on the two slopes during different times of the day and the season. Thus, habitat and season selection in relation to microclimate will be advantageous in balancing the energy budget, especially when overall food availability is low. However, selection pressures exerted by other factors (predation, snow, moult and migration) seem to be more dominant and, hence, may create a spatial and temporal pattern of breeding which deviates from the one predicted from metabolic considerations alone.

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